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# Evolution: Social Selection for Eccentricity

Dispatch

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**The dress code of paper wasps, like that of humans, is related to their social habits: species with a flexible nest-founding strategy have highly variable black-and-yellow markings. This color polymorphism facilitates individual recognition and might have been selected to permit complex social interactions.**

In nature, colorful patterns usually constitute a signal; they may deter competitors, frighten predators or attract mates. The standard view on animal signaling is that variation in ornamentation carries information about the condition and quality of the signaler [1,2]. For example, the black-and-yellow stripes of wasps are a signal of danger to other species. But there is more to it than that. A couple of years ago, Tibbetts [3] reported an experimental study showing that paper wasps use intraspecific variation in facial and abdominal markings to recognize individuals. A new comparative analysis by the same author [4] has revealed that species with a flexible nest-founding strategy have more variable markings than those with obligate single or multiple foundresses. This new work suggests that complex social interactions may select for individual distinctiveness and raises interesting questions about the costs and benefits of revealing individuality in social groups.

*Polistes* paper wasps form a widespread, species-rich group of social insects [5]. They build small, open paper nests in protected places. All paper wasps are eusocial: one or a few individuals monopolize reproduction, while other individuals defend the colony, forage and care for the brood [6]. After overwintering, mated females — the queens — found new nests. The species differ in their nest-founding habits, following one of three possible strategies: they may have an obligate single foundress, where only one queen starts a nest; they may have obligate multiple foundresses, where two or more queens start a nest together; or they may show flexible nest-founding, where either a single queen or multiple queens start a nest.

Paper wasp colonies are well known for having a dominance hierarchy [5,7,8]. In species with an obligate single foundress or obligate multiple foundresses, dominant queens usually monopolize all reproduction, and other females behave as workers. In species with a flexible nest-founding strategy, the social interactions tend to be more complex. There are even some theoretical and empirical indications that queens engage in reproductive transactions whereby they yield part of the reproductive potential to other females in order to make them stay and cooperate peacefully [9,10]. Complex alliances of this kind require that wasps are able to accurately recognize individuals.

*Polistes fuscatus* individuals have highly variable markings on their face and abdomen, such as the presence or absence of conspicuous yellow eyebrows [3]. Together, these markings yield dozens of unique patterns, suggesting they may serve for visual recognition of individuals. Indeed, wasps that had experimentally altered markings were found to receive more aggression than control wasps that had been painted without altering their markings [3]. Importantly, the aggression was transient and declined with time as wasps became familiar with the new markings. This elegant study showed that wasps use visual cues to distinguish individuals. Further, it suggested that variable markings might undergo selection for improved individual recognition in species with complex social interactions.

Tibbetts [4] explored whether social behavior selects for marking variability in *Polistes* using the comparative method, a powerful tool in evolutionary biology [11]. The idea is to examine if characters are distributed randomly on the branches of the cladogram representing the phylogenetic relationships of the species, or if given phylogenetic groups are more likely to share certain characters [12]. Tibbetts [4] used the method to test if marking variability is more likely to be gained and less likely to be lost in phylogenetically independent groups of species with a particular nest-founding strategy. She measured the degree of variability in museum specimens from 69 *Polistes* species. From the literature, she obtained data on the nest-founding strategies of 25 of these species; she then mapped the state of the two characters on a phylogeny of the group.

The observed distribution of marking variability revealed that low variation is the ancestral state, and that variable markings have evolved several times independently. More importantly, marking variability was strongly associated with nest-founding strategy. Variable markings were found in eight species with flexible nest-founding strategy. Thirteen species with obligate single or multiple foundresses were found not to have variable markings. The remaining four species have a flexible nesting-founding strategy but not variable markings. When controlling for the non-independence due to phylogenetic relationships, the test revealed that variable markings are more likely to be gained, and less likely to be lost, in species with a flexible nest-founding strategy.

What is the basis for this association between flexible nest-founding strategy and morphological variability? Tibbetts [4] proposes that variable markings have been selected for in species that have the most complex social interactions. Dominance hierarchies are likely to be easier to establish when individuals can be reliably and quickly recognized. Indeed, dominance hierarchies are best known in social mammals and birds, which have good individual recognition abilities [13,14]. Species with a flexible nest-founding strategy tend to

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have linear dominance hierarchies which determine how food, work and reproduction are divided among individuals. Species with obligate single or multiple foundresses also have dominance hierarchies, but one despotic queen tends to monopolize all reproduction. Arguably, the benefits of individual recognition, and thus the selection for marking variability, might be smaller in a society of this kind.

This argument is logically sound, but the premise that nest-founding strategy accurately reflects the complexity of social interactions remains somewhat speculative, particularly when comparing species with a flexible nest-founding strategy *versus* those with obligate multiple foundresses. Other characteristics associated with nest-founding strategy might also influence the use of visual recognition cues. For example, species might differ in colony size, darkness of nesting sites, colony genetic diversity or developmental stability. It would be of interest to test experimentally the hypothesis that variable markings reduce aggression and facilitate reproductive transactions. Manipulating the markings of queens with color paints and recording social interactions and colony productivity might reveal if individual distinctiveness is beneficial only in species with a flexible nesting strategy.

One might also question the idea that variable markings constitute an evolved signal, rather than an unselected cue [1]. Signals carry information about the emitter and alter the behavior of the receiver. For signaling to evolve, the receiver must on average benefit from behaving in a way that is also favorable to the emitter. Otherwise, the receiver should ignore the signal, or the emitter should stop signaling. Hence, stable signaling systems are expected to evolve when both parties have a strong common interest [1]. In paper wasps, colony members are usually related, and jointly benefit when an increase in colony productivity permits more copies of their genes to be transmitted to the next generation [15]. Selection might thus have favored colonies in which distinguishable individuals stick to clear roles, thus minimizing the costs of repeated assessments and aggressive contests.

Having distinctive individuals may also diminish the costs of recognition and risks of errors. But colonies are not genetically homogenous so there is still the potential for conflict [16], particularly when foundress queens are unrelated [17]. Open conflicts do indeed occur frequently in *Polistes* colonies, with dominant individuals coercing subordinates that are lazy or reproduce in excess [18]. When punishment occurs among individuals of various degrees of relatedness, it remains unclear whether signaling individuality is really beneficial to the subordinates in most cases. Alternatively, variable color markings might have primarily evolved for other purposes, for example to facilitate nestmate recognition. They might also be unfakeable cues resulting from developmental or environmental instability, rather than evolved signals [1]. Data on the proximate mechanisms generating variable markings and on the variation in markings within and between colonies should help to distinguish between these alternative hypotheses.

The suggestion that complex social interactions can select for variability among individuals in social groups has an interesting bearing on the maintenance of genetic and phenotypic variation in natural populations [19]. In the vast majority of cases, natural selection is stabilizing: it favors individuals close to the mean over those close to extremes, decreasing phenotypic variation. Individual recognition based on variable markings might be a special case where natural selection favors phenotypic diversity. Rare phenotypes might be fitter because they are distinct from most other phenotypes in the population. This negative frequency-dependent selection is analogous to that operating on the self-incompatibility locus present in many species of flowering plants [20]. When two plants share the same incompatibility allele, they cannot cross-fertilize. This means that plants with a new or rare allele have more success at mating, and their alleles spread through the population until a polymorphic equilibrium is reached. Similarly, colonies of paper wasps with eccentric queens that are easy to recognize might be more efficient and more productive than colonies with average, standard looking queens. Whether selection for distinctiveness plays a role in maintaining phenotypic diversity in other taxa with complex social interactions, like humans or wild dogs, remains to be investigated.

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